THE DEMOGRAPHY OF BARREN-GROUND GRIZZLY BEARS (*URSUS ARCTOS*) IN NUNAVUT AND THE NORTHWEST TERRITORIES

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PREAMBLE

This report was commissioned by the Government of the Northwest Territories, Department of Resources, Wildlife, and Economic Development, in September, 2000. The mandate was to provide an independent assessment of the demography of barren-ground grizzly bears inhabiting mainland Nunavut and the Northwest Territories, based upon previously collected data from grizzly bear captures and radio-sightings. We wrote this report without solicitation of comments from the Government of the Northwest Territories; this report rests on our own judgement. The conclusions contained in this report reflect the professional opinions of the authors without any form of editing or censuring by the Government of the Northwest Territories or any other concerned parties.

March 31, 2001

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EXECUTIVE SUMMARY

(1) In 1995, the Government of the Northwest Territories and the University of Saskatchewan initiated a multi-faceted research program into the ecology of barren-ground grizzly bears inhabiting the central Arctic. As part of the project, the Government of the Northwest Territories wished to document the demographics of the grizzly bear population. This objective defines the scope of research outlined in this report.

(2) Results are based upon an extensive satellite and VHF radio-telemetry program conducted for grizzly bears in a study area of approximately 235,000 km^2, centred 400 km northeast of the city of Yellowknife, Northwest Territories. We estimated survival rates, reproductive parameters, and the finite rate of increase of the population (λ) from these data. Using existing harvest and telemetry data, we then developed computer simulations to identify the potential risks for reducing the grizzly bear population in the region based on current harvest.

(3) Annual adult female survival was estimated at 0.979 (SE =0.012) while adult male survival was 0.966 (SE = 0.024). Cub-of-the-year (COY) survival was 0.737 (SE = 0.060) and yearling survival was 0.683 (SE = 0.074). COY litter size averaged 2.23 (SE = 0.13, n = 35), while yearling litter size decreased to a mean of 1.86 (SE = 0.12, n = 35). Mean litter size of females with two-year-old cubs was 1.85 (SE = 0.15, n = 20). Mean birth interval was 2.8 years (SE = 0.3, n = 17). Mean reproductive interval, which is calculated by excluding the loss of whole litters from the sample, was 3.9 years (SE = 0.4, n = 9). Mean litter size divided by the mean birth interval yielded an annual natality rate of 0.81 COYs per adult female per year. Mean age at first parturition was 8.1 years (SE = 0.5, n = 10). Mean age at first parturition, where at least one COY in a litter was successfully raised to at least age two, was 8.2 (SE = 0.7, n = 5). We believe the population to be currently stable or slightly increasing (λ = 1.033).

(4) Computer simulation models indicate that the population is at risk to population decline, especially if annual removal rates are increased from a mean of 13.4 bears/year. By adding only six animals to the mean removal rate, there is greater than a 40% chance of a decrease in

population size by one-quarter over the next 50 years, compared to only a 10% risk of decline under the current reported harvest. Unreported illegal mortality may already be contributing to a higher risk of population decline. We believe that communities, hunting camps, exploration camps, and mine sites must not contribute to a cumulative removal rate exceeding 15 bears/year in the study area. If removal rates exceed 15 bears/year, mitigation may necessitate a reduction in existing harvest quotas. We believe any increase in current harvest quotas would be detrimental to the population. Removal of females (and especially females with cubs) must be minimized from all sources of harvest. This is most important as removal rates used in our risk assessments are based on past patterns of harvest (1958–2000), and thus assume a subadult and male-biased harvest. If females with cubs contribute more to the reported harvest than in the past (i.e., as problem kills at mine sites or camps), risks of population decline will increase dramatically.

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1.0 INTRODUCTION

Although most grizzly bear (*Ursus arctos*) populations in North America have undergone some decline or range reduction subsequent to the arrival of Europeans, populations of barren-ground grizzly bears inhabiting Arctic regions have remained relatively undisturbed by European settlement. Far removed from human habitation, barren-ground grizzly bears have not been subjected to the exploitation and habitat changes that led to the extirpation of grizzly bears from much of their former range. Nonetheless, all populations of grizzly bears in Canada—including barren-ground populations—are classified as "vulnerable" and considered susceptible to population decline. This is largely because the species is slow to reproduce (late age at maturity, small litter sizes, long interbirth intervals) and is relatively rare (Committee on the Status Of Endangered Wildlife in Canada, 1991, List of species at risk, Canadian Wildlife Service, Ottawa, Ontario, Canada).

Barren-ground grizzly bears in Canada's central Arctic (Fig. 1.1) may be at particular risk to population decline for several reasons: (1) they have limited continuity with

other grizzly bear populations because they are near the northern and easternmost limit of the species' North American

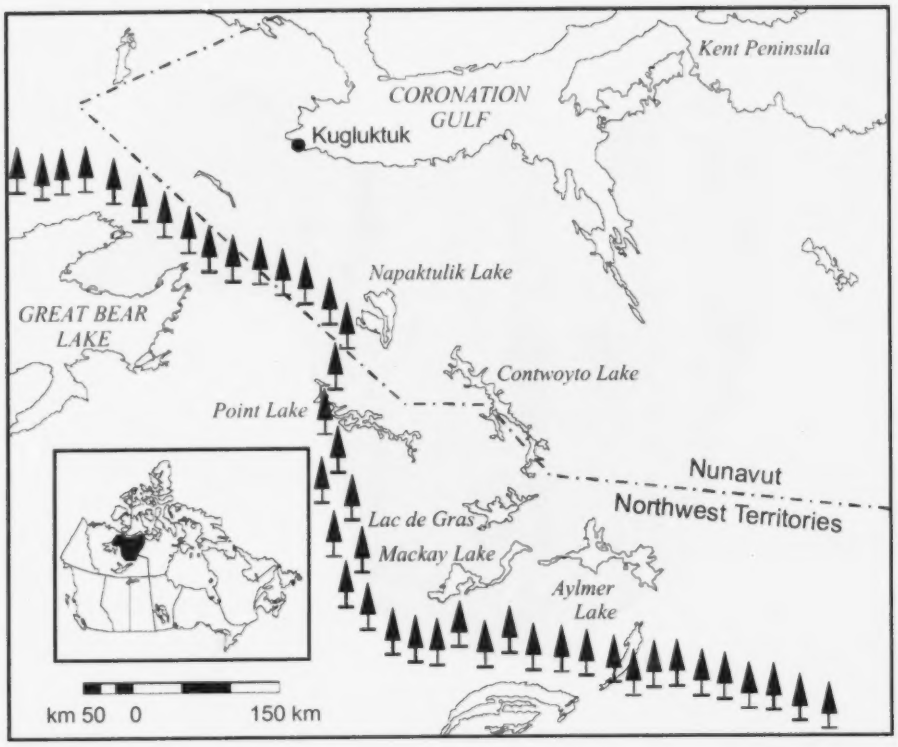

Fig. 1.1 Bounds of the study area used in this report (shaded region) in Canada's central Arctic. The treeline indicates the northernmost extent of coniferous forest in the study area.

range, (2) because of reduced cover, bears in tundra habitats are more likely to be displaced by nearby human activity than bears in forested areas (McLellan 1990), (3) populations of grizzly bears in tundra habitat exist at the lowest recorded densities of all extant North American grizzly bears (review in McLellan 1994), and (4) they have very large spatial requirements (Reynolds 1980; Nagy et al. 1983; Clarkson and Liepins 1989; Ballard et al. 1993; McLoughlin et al. 1999; McLoughlin 2000), which may expose individual bears to human activity even when developments are at a considerable distance from the core of the home range of an animal.

Recent discoveries of diamonds, gold, and base metals in the central Arctic have only added to concerns regarding barren-ground grizzly bear conservation in the region. The Governments of Nunavut and the Northwest Territories support exploration and mining as long as such activities do not unduly impact the environment or its wildlife populations. Agencies such as the Federal Department of Indian Affairs and Northern Development, First Nations groups, the World Wildlife Fund, and the Canadian Arctic Resources Committee have all recognized the need for a conservation strategy to protect barren-ground grizzly bears in the area. In

addition, mining companies (e.g., BHP Diamonds Inc., Diavik Diamonds Mines Inc.) have committed themselves to the concept of "sustainable development", thus supporting steps to mitigate the negative effects of resource exploration and extraction on barren-ground grizzly bears. Although it is agreed that grizzly bears in the central Arctic must be protected, knowledge of the ecology of bears in the region is limited and currently impairs the development of management strategies that would achieve this goal (Government of the Northwest Territories, 1991, Discussion paper towards the development of a Northwest Territories barren-ground grizzly bear management plan, Yellowknife, Northwest Territories, Canada).

In 1995, to address concerns about the potential effects of human developments on barren-ground grizzly bears, the government of the Northwest Territories and the University of Saskatchewan initiated a multi-faceted research program into the ecology of grizzly bears inhabiting the central Arctic. Specifically, the spatial organization, habitat and nutritional requirements, home range requirements, and denning requirements of grizzly bears in the central Arctic were studied (Gau 1998; McLoughlin 2000). In addition, the government of the

Northwest Territories wished to describe the demographics of the grizzly bear population. This objective defines the scope of research outlined in this report.

2.0 PROJECT OBJECTIVES

In this report we document the demography of barren-ground grizzly bears in the central Arctic. The general objective is to produce a "resource" report, rather than a "policy" report, that could be used in drafting a management plan for grizzly bears in the region. Data collected during an initial study of the demography of grizzly bears conducted in the northwest portion of the study area (Case and Buckland 1998), plus demographic data collected for the entire study area since 1995, provides the basis for the current project. The specific objectives are:

I. To collect and consolidate all information on capture (1988-2000) and kill (1958-2000) histories for barren-ground grizzly bears in the study area. These data summaries include:

   1) Standing age distribution based on captures of animals

2) Standing age distribution based on reported kills in the study area

3) Adult and subadult cohort histories from radio-telemetry studies

4) Reproductive histories of monitored females

II. To summarize population parameters of grizzly bears in the study area. These parameters include:

1) Adult female and male survival rates

2) Subadult female and male survival rates

3) Cub-of-the-year (COY) survival rates

4) Yearling survival rates

5) Mean litter sizes

6) Birth interval

7) Reproductive interval

8) Natality

9) Age at first parturition

10) Age at first parturition with successful rearing of at least one cub

11) Population rate of increase (λ)

12) Density and population size

III. To identify potential risks from harvest for reducing the grizzly bear population in the region using computer population projection simulations. We will incorporate existing harvest and telemetry data and estimated population parameters as input for our models.

3.0 METHODOLOGY OF ANALYSIS

3.1 Study Area

The study area was located in Canada's central Arctic, encompassing approximately 235,000 km^2 of mainland Nunavut and the Northwest Territories (Fig. 1.1). The study area was delineated, clockwise, by the community of Kugluktuk, the Kent Peninsula, Aylmer Lake, Mackay Lake, and Great Bear Lake. The region is characterized by short, cool summers and long, cold winters. Summer temperatures average 10°C and winter temperatures are commonly below -30°C. The area is semi-arid with annual precipitation around 300 mm, about half of which falls as snow (BHP Diamonds Inc., 1995, Ecological mapping: 1995 baseline study update, Yellowknife, Northwest Territories, Canada). Drainages support willow (*Salix* spp.) and dwarf birch (*Betula glandulosa*) shrubs as tall as three m, and birch shrublands (<0.5 m in height) dominate the uplands. Shrubs such as blueberry (*Vaccinium uliginosum*), cranberry (*Vaccinium vitis-idaea*), and crowberry (*Empetrum nigrum*) are common and their berries are important foods to grizzly bears (Gau 1998). The Bathurst caribou (*Rangifer tarandus*) herd migrates annually through the study area. The herd leaves wintering grounds below the

treeline in April, travels to calving grounds near Bathurst Inlet by early June, and disperses south in late summer and autumn. The herd was estimated at 349,000 ± 95,000 caribou >1 year of age in 1996 (Gunn et al. 1997). Muskox occur locally in the northern half of the study area. Much of the study area is part of a well-drained peneplain with lakes in the hollows and scattered depressions. Rounded rocky hills and glacio-fluvial features such as eskers, kames, drumlins, and raised beaches are often the only major relief features.

3.2 Animals and Telemetry

Satellite and VHF radio-telemetry (Telonics, Mesa, Arizona, USA, and Service Argos Inc., Landover, Maryland, USA) were used to obtain demographic data on barren-ground grizzly bears. Satellite telemetry provides continued and precise (approximately ±0.5 km, SD) information on bear movements with minimum disturbance to bears (Fancy et al. 1988; Harris et al. 1990). Satellite collars were equipped with a VHF beacon to permit relocations of radio-marked animals from an aircraft and, eventually, for the retrieval of collars. Most collars were designed to transmit approximately two to five locations every two days (eight-hour duty cycle) from 1 May to 1 November. During other

months, collars were programmed to transmit locations every eight days to minimize output of battery power.

Field personnel with the Government of the Northwest Territories and the University of Saskatchewan used a Bell 206B or Hughes 500 helicopter to search for and capture bears. A Piper SuperCub, Scout, or Aviat Husky aircraft equipped with skis or floats was sometimes used for more intensive searches of the study area. Most grizzly bears were captured in spring during the snow melt period (15 May–5 June) by following tracks in the snow (Case and Buckland 1998). Each bear was immobilized with an injection of titelamine hydrochloride and zolazepam hydrochloride (Telazol®, Ayerst Laboratories Inc., Montreal, Quebec, Canada) from a projected dart. Immobilized animals were marked with identification numbers applied as ear tags and permanent lip tattoos. Bears were weighed using a load-cell scale (Norac Systems International Inc., Saskatoon, Saskatchewan, Canada) while suspended in a cargo net from a helicopter. Heart girth, straight-line body length, skull length, and skull width were measured with a tape measure and calipers, and a vestigial premolar tooth was extracted for age determination (Craighead et al. 1970). Some bears were tested for nutritional condition using bioelectrical

impedance analysis and blood sampling (Gau 1998). Only those bears weighing ≥110 kg (males) and ≥90 kg (females) were fitted with radios before release.

3.3 Capture, Kill, and Reproductive Histories

We obtained records of grizzly bear captures from the Department of Resources, Wildlife, and Economic Development (years 1988–2000) and field notes associated with McLoughlin (2000). Records of legal harvest, problem kills, and suspected illegal mortalities for the region were obtained from internal records of the Department of Resources, Wildlife, and Economic Development (years 1958–2000). Telemetry data and field notes used by McLoughlin (2000) provided the basis for the compilation of reproductive histories for monitored female grizzly bears (e.g., presence/absence of accompanying young, ages of accompanying young).

Data were summarized into tables detailing the standing age distributions (reference) based on capture records and kills. Reproductive histories of female grizzly bears were compiled into a table depicting the reproductive status of monitored females by observation year (Case and Buckland 1998).

3.4 Demographic Parameters

3.4.1 Survival Rates

Survival rates can be specific for every sex and age class in the population under study; however, in practice strata of age-constant rates can be identified for both males and females. These strata typically include age zero (i.e., recruits), subadult (i.e., pre-reproductive), adults (i.e., reproductively mature), and senescent ages. In this study we use age zero (cub-of-the-year, or COY), age one (yearling), subadult (ages 2-4), and adult (ages ≥5) categories.

There are several possible methods for estimating annual survival rates. These include analysis of the standing age distribution and cohort analyses. Caughley (1977) provides a clear explanation of the difficulties in determining survival rates from the standing age distribution. Essentially, it cannot be done unless the population growth rate is already known and the population is at stable age distribution.

Cohort estimates of survival may be obtained in two main ways. The first cohort method of estimating survival stems from mark-recapture analysis. There are several

excellent reviews of the considerations for mark-recapture estimates of population numbers and survival (Cormack et al. 1979; Nichols et al. 1981; Pollock 1981; Seber 1982; Pollock et al. 1990; Skalski and Robson 1992; and Lancia et al. 1994; Krebs 1999). Implementation of this method requires the meeting of a number of assumptions. For example, the capture and recapture effort must allow for every animal in the population to have an equal chance to be captured. This assumption can be difficult to meet when the vulnerability to trapping or aerial capture differs for some sex and age classes, and probably was not met in the data available for estimating survival rates. Thus, mark-recapture methods were not applied to estimate survival rates in this study.

The second cohort method to obtain survival rates, and that used in this study, is by following individuals through time (typically by using radio telemetry). Several models have been used to analyze mortality schedules obtained from following individuals with radio collars (Trent and Rongstad 1974; Heisley and Fuller 1985; Pollock et al. 1989; Amstrup and Durner 1995). These methods have some drawbacks, however, particularly for estimating adult survival rates when adult survival is high. For example, with telemetry studies of mortality rates, dead individuals may have a

higher probability of being undetected than live individuals. Starving individuals may disperse from the study area, may burrow into dens which retard or eliminate radio signals, or may die in rivers lakes, oceans, or ice, and sink. If a larger fraction of these missing radios are dead bears, in contrast to radios on live bears, mortality rates are underestimated by procedures that censor silent radio beacons as missing data.

From telemetry data, we calculated several survival rates to separately evaluate natural and human-caused mortality, and the possible effects of missing radios in cohort histories on survival. These scenarios involved calculations of survival rates by: (1) including only confirmed natural mortalities in survival rates; (2) including natural mortality plus all missing radios as unconfirmed mortalities in survival rates; (3) including all natural, plus all known legal or illegal kills (including capture mortalities) in survival rates; and (4) including all sources of confirmed mortalities plus unconfirmed mortalities in survival rates. We did not use data from bears for which monitoring could not be maintained between recaptures (i.e., through the loss of a radio, $n = 1$), which may lead to inflated estimates of survival rates because

only surviving bears for whom contact was lost can be recaptured (White and Garrot 1990, pp. 224-225; Hovey and McLellan 1996).

For comparison purposes we used two estimators to calculate adult mean annual survival. First, we used Pollock et al.'s (1989) staggered-entry modification of Kaplan and Meier's (1958) survivorship model because of its broad basis in survival theory and widespread use among bear researchers (e.g., Amstrup and Durner 1995; Hovey and McLellan 1996). We determined cumulative survival at seasonal intervals as in Amstrup and Durner (1995) by determining the number of new radios applied, total number of radios at risk, total number of radios censored, and total number of deaths from tables of tracking histories. Pollock et al's (1989) model estimates a cumulative survival rate, variance, SE, and confidence interval for an entire period of study (here, 11.5 years for adult females and 4.5 years for adult males). We converted survival estimates for the duration of monitoring to mean annual survival with 95% confidence intervals (CI) by taking the 11.5^{th} and 4.5^{th} roots of the total survival point and 95% confidence limit estimates for adult females and males, respectively (see Amstrup and Durner 1995).

Second, for adult females and males, as well as for subadult females and males for which sample sizes were too low to use Pollock et al's (1989) procedure, we determined mean annual survival (SE and 95% CI) according to methods presented in Trent and Rongstad (1974). This binomial estimator is also widely used (see White and Garrot 1990; for grizzly bears, Eberhardt et al. 1994), and offers the advantage of providing a standard error (SE) for mean annual survival rates. No SE is calculated for annual Kaplan-Meier means: only the SE associated with the mean survival of animals over an entire period of study is available, which cannot be converted to an annual SE by taking its n^{th} root, where n equals the number of years in the period of study (although annual means and a CI associated with the annual mean can be obtained by taking the n^{th} root of the cumulative mean and its confidence limits—see above). Here, mean annual survival was determined by the formula:

[3.1] S = 1 - recorded deaths/bear-years observed

The annual survival rates of COYs and yearlings were calculated as one minus the division of cub deaths (Dc) and number of cubs observed (Rc)(Eberhardt et al. 1994; Hovey and McLellan 1996):

[3.2] $S = 1 - Dc/Rc$

We calculated SE and 95% CI as in Trent and Rongstad (1974). By using this estimate we assumed the disappearance of a cub (including yearlings) at some time between one spring census and the next equated to the cub's death (Case and Buckland 1998). To prevent introducing bias, our calculations of cub survival used only cubs of mothers that were radio-tracked for the entire year and into the next active season. Records of cubs whose mothers were tracked <1 year were ignored whether of not cubs died.

3.4.2 Reproduction

Litter size was determined from the number of cubs first observed with a female in the spring or early summer. We defined birth interval as the number of years between the birth of cubs, including intervals shortened by whole litter loss. Reproductive interval was the number of years between successful litters (i.e., those litters for which at least one cub survived to two-year-old status). Natality was estimated by dividing mean litter size by mean birth interval, and represents the average number of cubs produced

per female per year in the population. From reproductive histories, we determined the mean age at first parturition. We also determined the mean age at first parturition leading to the successful rearing of at least one cub to two-year-old status.

3.4.3 Population Rate of Increase

The finite rate of population increase (λ) was estimated from reproductive rates and female survival rates obtained from confirmed natural plus confirmed human-caused mortality. We used an approximation of Lotka's equation proposed by Eberhardt (1985), and as presented in Eberhardt et al. (1994):

$$[3.3] \qquad \lambda^{a} - S_{adult}\lambda^{a-1} - l_{a}m[1 - (S_{adult}/\lambda)^{w-a+1}] = 0$$

Where S_{adult} is mean annual adult female survival rate, l_a is survival to mean age of first parturition (a), w is the maximum age considered, and m is the number of female cubs per adult female per year (i.e., natality rate multiplied by 0.5). We solved for λ by iteration. The parameter w was fixed at 25 years.

3.4.4 Density and Population Size

We developed a crude estimate of density and population size for the study area based on the suspected minimum number of bears inhabiting a central, 14,000 km^2 regional study area (RSA) in the vicinity of Lac de Gras (Fig. 1.1). We developed the estimate based on the numbers of collared and uncollared bears thought to be residents in the RSA during 1997, at the height of the collaring and monitoring effort in the Lac de Gras region. To obtain our estimate of total population size, the density estimate for the RSA was extrapolated to the entire study area (235,000 km^2). The estimate assumed a uniform density of bears across the study area, which is not likely. It is possible that a higher density of bears in the Kugluktuk region may "cancel out" suspected lower densities of bears in the Bathurst Inlet/Eastern parts of the study area (Fig. 1.1). The estimate should be regarded as only a preliminary estimate of population size.

3.5 Risk Analysis

3.5.1 Background

Management recommendations, particularly harvest policies, are often based on life table models of population

dynamics. Estimates of population size, sex and age distribution, survival, recruitment, and harvest (if any) may be used in age-structured, birth-pulse simulation models to estimate: population trend or status, number at some future time, and to explore the demographic consequences of a range of management options. Models may allow both exponential growth and density dependent feedback mechanisms. Harvest can be modelled in a variety of ways, ranging from detailed simulations that include the age-specific vulnerability and selectivity of the kill to simple apportionment of the kill according to the abundance of the population sex and age types. A WINDOWS© compatible program named RISKMAN (RISK MANagement) was developed for the full range of options described above (Taylor et al. 2001). Here we use RISKMAN to model risks of population decline for barren-ground grizzly bears in the central Arctic.

Deterministic population projections are sometimes difficult to interpret because all results are based on very uncertain estimates of input parameters, and cannot be objectively distinguished from results based on relatively precise estimates of input parameters. RISKMAN provides a stochastic option that uses the variance of input parameters and the structure identified by the simulation options that

are selected. Here we use Monte Carlo techniques to generate a distribution of results, and RISKMAN uses this distribution to estimate the variance of summary parameters (e.g. population size at a future time, population growth rate, and proportion of runs that result in a population decline set at a pre-determined level by the user). RISKMAN utilizes the correct distributions of the population and rate variance estimates to provide estimates of the uncertainty of simulation results.

3.5.2 Input Required by RISKMAN

Input required to run population projection models to estimate growth rates and risks of population decline were obtained from calculations and tables developed according to sections 3.3 and 3.4, above. Required input data included: (1) estimates of male and female survival rates plus their standard errors (SE) for adults, subadults, yearlings, and COYs. For females, survival rates were separated into age-specific strata including unencumbered females, females with one COY to three COYs, females with one yearling to three yearlings, females with one two-year-old to three two-year-olds; (2) age-specific probabilities of females with new litters having one, two, or three COYs in their litters; (3)

mean proportion of females of age *x* that were available for mating in year *x* - 1 and gave birth to a litter in year *x*, plus SE; (4) mean proportion of males at birth, plus SE; (5) estimates of minimum and maximum ages of reproduction; (6) an array that contained all known harvest and defense kills that was compared to the stable age distribution (calculated by RISKMAN) to get an estimate of the current relative selectivity and vulnerability of the various sex/age/family-status strata to harvest mortality; (7) the mean annual removal rate as individuals per year (i.e., annual harvest rate); and (8) initial population size of the population under study, plus a SE associated with the estimate. Finite rate of population increase is not a required input by RISKMAN, as it is calculated by the program itself. Although there are provisions to model density-dependent effects in RISKMAN, we had no data to model such effects at the time of writing this report.

3.5.3 Models Produced Using RISKMAN

We created RISKMAN models to document the potential risk from harvest to generate a decline in the grizzly bear population. We estimated the probability of the grizzly bear population declining by 25%, 50%, and 75% of the

current population size over a specified time interval of 50 years from present. To examine the risks of increasing current harvest, or to account for possible risks of unreported illegal harvest, we ran simulations with the mean annual harvest rate increased by six bears annually (e.g., increasing quotas in both Kugluktuk and Umingmaktok by 3 bears/year each). To account for uncertainty in our survival data, we ran simulations that decreased estimates of rate of increase by including bears that went missing during our monitoring program as unconfirmed mortalities.

RISKMAN is designed to provide Monte Carlo estimates of the uncertainty of simulation results using the variance of input parameters. Our rationale for model structure and approach to variance is summarized in Taylor et al. (2001). We ran 2,800 stochastic simulations for each year of a simulation to provide a distribution of model outcomes (i.e., population numbers at survey time) from which risks of population declines were estimated.

4.0 RESULTS

4.1 Capture, Kill, and Reproductive Histories

4.1.1 Standing Age Distribution: Captures of Animals

From May 1988 to June 1999, 283 barren-ground grizzly bears were immobilized by capture crews on at least 330 occasions. Of these 283 individuals, 106 were adult females and 53 were adult males. Among subadults (aged three to four years), 12 were females and 20 were males; three subadults of unknown sex were also captured. We identified 30 cubs-of-the year (17 females, 14 males, 10 unknown sex), 16 yearling cubs (nine females, 10 males, 20 unknown sex), and nine two-year-old cubs (three females, six males). In the period 1988–1991, 15 VHF radio-collars were placed on females in the Kugluktuk region of the study area (Fig. 1.1; Case and Buckland 1998). From 1995–1998, researchers placed 89 satellite radio-collars on 81 bears (n = 38 adult females, n = 4 subadult females, n = 35 males, n = 4 subadult males). For 23 of these bears (mostly females), "break-away" VHF radio-collars were fitted after satellite radio-collars were removed.

We assembled data on capture records into a table to depict the standing age distribution of the population based

on total captures of animals, 1988-1999 (Table 4.1).

Standing ages were skewed towards females, likely due to a

Table 4.1 Pooled standing age distribution summarizing grizzly bear captures in the central Arctic, 1988-1999.

AGE	Male	F No cub	F 1 COY	F 2 COY	F 3 COY	F 1 yrlg	F 2 yrlg	F 3 yrlg	F 1 2yr	F 2 2yr	F 3 2yr	F 1 3yr	F 2 3yr	F 3 3yr	Sex Unk	TOTAL
0	14	17													10	41
1	10	9													20	39
2	15	7													2	24
3	6	4													1	11
4	5	4														9
5	4	7	1													12
6	11	11														22
7	6	6					1									13
8	1	3		1					1	1						7
9	4	5				1										10
10	3	6		1	1	2	1			1	1					16
11		5					1		1	2						9
12	2	1		2				1								6
13	2	1			2		1	1								7
14	4	1		1		1	3									10
15	4	5						2								11
16	1	1		2	1		1									6
17	1			1	1					1						4
18	1															1
19	1	1			2											4
20	2	1					1							1		5
21	1	2					1									4
22	1	1	1													3
23	1					1	1									3
24	2		1													3
25	1	1	1													3

TOTAL	103	99	4	8	7	5	11	4	2	5	1	0	0	1	33	283

male-biased harvest (see below) and possibly because females with cubs may be easier to track or visualize during capture efforts to distribute new radios.

4.1.2 Standing Age Distribution: Harvest Data

We assembled data on harvest records (112 problem, 55 regular, 47 sport, one subsistence, two illegal, 48 unknown cases) into a table to depict the standing age distribution of the population based on the total kills of animals (Table 4.2). Only field ages (adult, subadult, cubs aged 1-3, and COY) are reported in the harvest records. Harvest records were highly skewed towards adult and subadult males.

4.1.3 Adult Female Telemetry Cohort Data

We compiled the histories of adult female grizzly bears radio-tracked for years 1988-1999 into Table 4.3. Notes on survival for these animals can be found in section *4.2.1.*

4.1.4 Adult Male Telemetry Cohort Data

We assembled capture and monitoring histories for adult male grizzly bears followed by telemetry for years 1995-1999 (Table 4.4). Notes on survival for these bears can be found in section *4.2.1.*

Table 4.2 Pooled standing age distribution summarizing grizzly bear kills for reporting stations at Kugluktuk, Umingmaktok, Lupin, Rae, and Yellowknife, 1958–2000.

AGE	Male	F No cub	F 1 COY	F 2 COY	F 3 COY	F 1 cub1-3	F 2 cub1-3	F 3 cub1-3	Sex Unk	TOTAL
COY	2									2
Cub1-3	16	8							4	28
Subadult	46	20							21	87
Adult	84	24					4		10	122
Unk	6	3							17	26
TOTAL	154	55	0	0	0	0	4	0	52	265

Table 4.3 History of adult female grizzly bears followed by satellite and VHF radio-telemetry, 1988–1999. The coding scheme is: 1 = bear alive with working radio; D = bear dead due to natural mortality; K = bear killed due to harvest; S = suspected illegal mortality; R = radio purposely removed from bear, or radio dropped; M = radio and bear missing; C = capture mortality. Table continues onto the next page.

Year	1988		1989		1990		1991		1992		1993		1994		1995		1996		1997		1998		1999	
Bear	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
G501	1	1	1	1	1	1	1	1	1	1	1	1	1	1	R									
G502	1	1	1	1	1	1	1	1	1	1	1	D												
G505	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	R				
G511			1	1	1	1	1	1	1	1	1	1	1	1	1	R								
G514			1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	M					
G517			1	1	1	1	1	1	1	1	1	1	1	1	1	R								
G522					1	1	1	1	R								1	1	1	1	R			
G524					1	1	1	1	1	1	1	1	1	1	1	1	1	1	M					
G534					1	1	1	1	1	1	1	1	1	1	1	1	1	1	M					
G535					1	1	1	1	1	1	1	D												
G541							1	1	1	1	1	1	1	1	1	1	1	1	1	R				
G543							1	1	1	1	1	1	1	1	1	1	1	1	1	R				
G549							1	1	1	1	1	1	1	1	1	R								
G592															1	1	1	1	R					
G597															1	1	1	1	R					
G601															1	1	1	1	R					
G604															1	1	1	1	R					
G605															1	1	1	1	R					
G606															1	1	1	1	R					
G611															1	D								
G614																	1	1	M					
G627																1	M							
G638																	1	1	1	1	1	1	1	R
G639																	1	1	1	1	1	1	1	R

Year	1988		1989		1990		1991		1992		1993		1994		1995		1996		1997		1998		1999	
Bear	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
G640																	1	1	1	1	1	1	1	R
G642																	1	1	1	1	1	1	1	R
G643																	1	1	1	1	1	1	1	R
G646																	1	1	1	1	1	1	1	R
G648																	1	1	1	1	R			
G649																	1	1	1	1	R			
G650																	1	1	1	1	R			
G652																	1	1	1	1	1	1	1	R
G663																			1	1	1	1	1	R
G681																			1	1	1	R		
G683																			1	1	1	1	R	
G684																			1	1	1	1	1	R
G686																			1	1	1	1	R	
G695																					1	1	1	R
G701																					1	1	R	
G702																					1	1	1	R
G721																					1	1	1	R
G726																					1	1	1	C
G731																					1	1	1	R

Table 4.4 History of adult male grizzly bears followed by satellite and VHF radio-telemetry, 1995–1999. The coding scheme is: 1 = bear alive with working radio; D = bear dead due to natural mortality; K = bear killed due to harvest; S = suspected illegal mortality; R = radio purposely removed from bear, or radio dropped; M = radio and bear missing; C = capture mortality.

Year	1995		1996		1997		1998		1999	
Bear	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
G530			1	1	1	1	R			
G595			1	1	R					
G603	1	1	1	1	M					
G612			1	1	1	R				
G613	1	1	1	1	R					
G618	1	1	1	1	M					
G619	1	1	1	1	R					
G626		1	1	1	R					
G630			1	1	1	1	R			
G631			1	1	1	1	R			
G637			1	1	1	R				
G644			1	1	1	1	1	1	R	
G647			1	1	1	1	R			
G653			1	1	1	1	1	1	1	R
G654			1	1	1	1	1	1	1	R
G655			1	1	1	1	R			

Year	1995		1996		1997		1998		1999	
Bear	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
G656			1	1	S					
G657			1	1	1	R				
G661					1	1	S			
G662			1	1	1	1	1	1	1	R
G664					1	1	1	R		
G680					1	1	1	R		
G682					1	1	1	D		
G689					1	1	1	1	R	
G690					1	1	1	R		
G691					1	1	1	R		
G696							1	1	R	
G697							1	1	1	R
G698							1	1	1	R
G706							1	1	1	R
G720							1	1	R	
G730							1	1	1	R

4.1.5 Subadult Female Telemetry Cohort Data

We compiled data on the history of subadult female grizzly bears followed by telemetry for years 1988–1999 (Table 4.5). Because we did not collar dispersing young, data on subadult female histories was sparse. Most subadult females were too small to collar (<90 kg), so only a few subadult females were monitored after their release from capture (n = 4, comprising five bear-years of data).

4.1.6 Subadult Male Telemetry Cohort Data

We compiled data on the history of subadult male grizzly bears followed by telemetry for years 1995–1999 (Table 4.6). Sample size was again low (n = 4, comprising five bear-years of data), for the same reasons as above.

4.1.7 Reproductive Histories of Monitored Females

We were able to obtain data on the reproductive histories of 56 female grizzly bears of various ages (Table 4.7). The earliest age at which a female was observed to produce a cub was five years (G592), indicating successful mating at age four (see section *4.2.2* for mean age of first parturition). This cub disappeared, however, the following summer. Reproduction appeared to continue throughout life,

Table 4.5 History of subadult female grizzly bears followed by satellite and VHF radio-telemetry, 1988–1999. Coding scheme is: 1 = bear alive with working radio; A = bear aged into adult category; D = bear dead due to natural mortality; K = bear killed due to harvest; S = suspected illegal mortality; R = radio purposely removed from bear, or radio dropped; M = radio and bear missing; C = capture mortality.

Year	1988		1989		1990		1991		1992		1993		1994		1995		1996		1997		1998		1999	
Bear	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
G507	1	1	K																					
G591															1	R								
G614															1	1	A							
G651																	1	R						
G660																		1	1	1	1	1	A	
G685																			1	R				
G705																					1	R		
G724																					1	S		

Table 4.6 History of subadult male grizzly bears followed by satellite and VHF radio-telemetry, 1995–1999. Coding scheme is: 1 = bear alive with working radio; D = bear dead due to natural mortality; K = bear killed due to harvest; S = suspected illegal mortality; R = radio purposely removed from bear, or radio dropped; M = radio and bear missing; C = capture mortality.

Year	1995		1996		1997		1998		1999	
Bear	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
G595	1	1	A							
G600	1	1	1	1	R					
G612	1	1	A							

G700		1	1	K

Table 4.7 Reproductive histories determined in spring and early summer of female grizzly bears followed by satellite and VHF radio-telemetry, 1988–1999. Coding scheme is: NC = no cubs present; *n*COY = number of coys present; *n*YRLG = number of yearlings present; *n*2YR = number of two-year-olds present; *n*3YR = number of three-year-olds present; NO = not observed. The table continues over the next three pages.

			Reproductive Status In Spring of Observation Year, with notes on cub survival to next spring									
Bear	Year Captured	Age at Capture	1	2	3	4	5	6	7	8	9	10
G501	1988	6	NC	NC	2COY	2YRLG	22YR	1COY[a]	2COY	2YRLG		
G502	1988	22	NC	NC	1COY[a]	1COY[c]	NO	1YRLG[e]	DIED			
G505	1988	7	NC	NC	NC	3COY	3YRLG	32YR	NC	NC	NO	3COY
G507	1988	4	NC	Killed								
G511	1989	8	NC	3COY[a,f]	1YRLG	12YR	4COY[a]	3YRLG	32YR			
G514	1989	9	1YRLG[b]	2COY	2YRLGd	12YR	13YR	3COY	3YRLG	NO		
G517	1989	6	NC	NC	NC	2COY	2YRLG[d,f]	NC	NC			
G522	1990	14	2YRLG	22YR								
G524	1990	10	2YRLG[d,f]	NC	2COY	2YRLG	22YR	NC	NO			
G529	1990	13	NC									
G534	1990	6	NC	NC	3COY	3YRLG[d]	22YR	NC	NO			
G535	1990	15	NC	2COY	2YRLG	22YR	DIED					
G541	1991	6	NC	NC	2COY[a]	1YRLG[d]	NC	NO	2YRLG			
G543	1991	16	2COY[a]	1YRLG[d]	NC	2COY	2YRLG	NO	2YRLG			
G549	1991	13	3COY	3YRLG[d]	22YR	3COY	3YRLG					
G591	1995	3	NC									
G592	1995	5	1COY	1YRLG[b]	NO	NO	NO	NC				
G597	1995	11	12YR	NC								
G601	1995	19	3COY[a]	2YRLG								
G602	1995	10	1YRLG									

			Reproductive Status In Spring of Observation Year, with notes on cub survival to next spring								
Bear	Year Captured	Age at Capture	1	2	3	4	5	6	7	8	9
G604	1995	6	NC	NC							
G605	1995	10	32YR	NC							
G606	1995	5	NC	NC							
G608	2000	5	NC								
G611	1995	5	NC	Cap mort							
G614	1995	4	NC	NC							
G627	1995	5	NC								
G634	1996	16	NC								
G638	1996	10	NC	2COY[a,f]	NC	3COY					
G639	1996	11	22YR	NC	NC	2COY					
G640	1996	14	1YRLG	12YR	13YR	3COY					
G641	1996	7	NC								
G642	1996	6	NC	NC	NC	NC					
G643	1996	7	NC	NC	NC	3COY					
G646	1996	22	1COY	1YRLG	12YR	1COY					
G648	1996	6	NC	NC							
G649	1996	8	12YR	NC							
G650	1996	19	3COY	3YRLG							
G652	1996	14	2YRLG	22YR	23YR	2COY					
G660	1996	2	NC	NC	NC	NC					
G663	1997	19	NC	NC	NC						
G681	1997	9	NC	NC							
G683	1997	6	NC	NO							
G684	1997	21	NC	2COY[a]	1YRLG						
G685	1997	3	NC								
G686	1997	16	2COY[a]	1YRLG							

			Reproductive Status In Spring of Observation Year, with notes on cub survival to next spring									
Bear	Year Captured	Age at Capture	1	2	3	4	5	6	7	8	9	10
G695	1998	7	NC	NC								
G699	1998	10	NC									
G701	1998	25	NC									
G702	1998	16	2YRLG	22YR								
G705	1998	4	NC	NC								
G707	1998	9	1YRLG									
G721	1998	7	2YRLG	22YR								
G724	1998	2	NC	Susp collar								
G726	1998	11	NC	2COY[g]	Cap mort							
G731	1998	9	NC	2COY								
G746	1999	Unk	22YR									
G755	2000	Unk	2YRLG[b,f]									

[a] COY went missing during year and presumed dead

[b] Yearling went missing during year and presumed dead

[c] COY must have died for bear to give birth to another COY the following spring. Bear observed last with COY and accompanying adult bear (male?)

[d] Death of yearling if we assume they are dead if not found in spring census with mother when they are 2YR

[e] Death of mother tells us death of yearling

[f] At least two cubs lost in litter

[g] COYs euthanized as a result of capture mortality of G726

although it may have diminished at older ages. The oldest female (G502) in the study produced a cub at age 26 and was observed with a yearling just prior to her death the next year. The fate of the yearling was not known. Although this female was reproductively active after age 22, she contributed little more to the population, as two litters were lost as COYs and her last cub probably had a low chance of survival on its own. Another female, however, produced a cub at 22, weaned the cub successfully, and produced another COY at age 25 (at which time her radio was removed). A third female produced two COYs also at age 22, of which only one survived to yearling status before her radio was removed at age 23.

4.2 Demographic Parameters

4.2.1 Survival Rates

Three adult females were known to have died of natural causes during 146 bear-years of observation (1988–1999); however, five females went missing during the study and their collars were not recovered. It is therefore possible that eight females died from 1988–1999. We would caution, however, that this latter scenario is not likely and is probably underestimating natural female survival. Of the

five adult females that went missing, four disappeared in the spring of 1997 (Table 4.3), two years after their initial capture and near the end of the advertised lifespan of the batteries of their satellite radio-collars. It is highly possibly that these females survived but were not detected in our spring census due to malfunction of their satellite radio-collars. The number of missing females at the end of 1997 would have been higher if we had not located a number of females (n = 3) with malfunctioning collars by blindly searching for VHF beacons, of which each satellite radio-collar was also equipped (with a separate battery supply). This result indicates that missing collars often relate to live bears, not mortalities.

The three females that were confirmed to have died of natural causes were all suspected to have been killed by other, possibly male, grizzly bears. One female (G502) was found dead near her den, which had been excavated by another grizzly bear. Mounds of torn-up vegetation, characteristic of grizzly bear caches, and bear scats containing bear fur and bones were found in the areas where all three females died. One further adult female suffocated in a landslide during a capture operation in 1999. In general, Kaplan-

Meier estimates of natural survival were higher than binomial estimates (Tables 4.8 and 4.9, respectively).

Only one adult male was suspected to die a natural death (cause unknown) during 58 bear-years of observation (1995–1999). Two other males went missing during the study,

Table 4.8 Annual survival rates (mean with 95% confidence limits) of adult female grizzly bears using Pollock et al.'s (1989) staggered-entry modification of Kaplan and Meier's (1958) survivorship model.

	Survival[a,b]	95% Low	95% High
Confirmed natural mortality only	0.979	0.955	0.998
Confirmed natural + missing collars added as unconfirmed natural mortality	0.957	0.924	0.981
Confirmed natural + G627's capture mortality	0.972	0.946	0.993
All sources of confirmed and unconfirmed mortality	0.951	0.916	0.976

[a] No SE is calculated for *annual* Kaplan-Meier means. Only the SE associated with the mean survival of animals over the entire period of study (11.5 years) is available (see text).
[b] There was no confirmed legal or illegal harvest of adult females during the study.

Table 4.9 Annual survival rates (mean, SE, and 95% CI) of adult female grizzly bears using the methods of Trent and Rongstad (1974).

	Survival	SE	95% Low	95% High
Confirmed natural mortality only	0.979	0.012	0.940	0.996
Confirmed natural + missing collars added as unconfirmed natural mortality	0.945	0.019	0.894	0.976
Confirmed natural + G627's capture mortality	0.973	0.014	0.931	0.992
All sources of confirmed and unconfirmed	0.938	0.020	0.885	0.971

mortality

so it is possible that a total of three adult males died from 1995-1999. Again, we would caution that the latter scenario is probably underestimating natural male survival. Both missing males disappeared in the spring of 1997, as did the four of five missing females (Table 4.3), two years after their initial capture and likely beyond the lifespan of their satellite radio-collars. It should be noted that an adult male that also went missing at the end of 1997 (G618), and suspected of wearing a radio with a weak battery, was harvested in 1998. The bear was still wearing its satellite radio-collar, without any reported ill effects to the bear. G618 was subsequently removed from the "missing" list.

Two adult males are suspected to have died of illegal harvest during the monitoring period. In both circumstances, satellite radio-collars belonging to the bears were found in the field, opened up with all ny-lock fastening nuts removed. Both collars were in good shape. Note that these two possible illegal harvests were not included in Table 4.2.

As for adult females, Kaplan-Meier estimates of natural survival of males were slightly higher than binomial estimates (Tables 4.10 and 4.11, respectively).

For both adult females and males, high overlap of 95% CI strongly suggests that differences between methods of

Table 4.10 Annual survival rates (mean with 95% confidence limits) of adult male grizzly bears using Pollock et al.'s (1989) staggered-entry modification of Kaplan and Meier's (1958) survivorship model.

	Survival[a]	95% Low	95% High
Confirmed natural mortality only	0.986	0.942	1
Confirmed natural + missing collars added as unconfirmed natural mortality	0.962	0.889	1
Confirmed natural + suspicious collars added as human-caused mortality[b]	0.974	0.914	1
All sources of confirmed and unconfirmed mortality	0.949	0.865	1

[a] No SE is calculated for *annual* Kaplan-Meier means. Only the SE associated with the mean survival of animals over the entire period of study (11.5 years) is available (see text).

[b] There were two possible illegal mortalities of adult males in the study, as determined from the discovery of suspiciously dropped collars (see text).

Table 4.11 Annual survival rates (mean, SE, and 95% CI) of adult male grizzly bears using the methods of Trent and Rongstad (1974).

	Survival	SE	95% Low	95% High
Confirmed natural mortality only	0.983	0.017	**0.907**	**0.999**
Confirmed natural + missing collars added as unconfirmed natural mortality	0.948	0.029	**0.856**	**0.989**
Confirmed natural + suspicious collars added as human-caused mortality	0.966	0.024	**0.880**	**0.996**
All sources of confirmed and unconfirmed	0.931	0.034	**0.832**	**0.981**

mortality

estimating mean survival rates are statistically insignificant.

Small sample sizes precluded a meaningful analysis of subadult female survival rates. From five bear-years for which subadult females were monitored after being released from capture, one harvest mortality and one suspected illegal mortality (recovered collar with missing ny-lock nuts, as above) were observed. No natural mortalities were observed. Because of small sample sizes, we calculated survival rates for subadults according to the methods of Trent and Rongstad (1974) only. Mean total survival for subadult females was equal to 0.600 (SE = 0.235). Mean natural survival was 1.0, as no natural mortality was observed.

As for subadult females, small sample sizes made it difficult to estimate subadult male survival. For five bear-years of observation, one subadult male was killed due to legal harvest. Mean survival rate (total) was 0.800 (SE = 0.200). Mean natural survival was 1.0.

Of 57 COYs, 42 (74%) survived to their next year, providing a mean survival rate of 0.737 (SE = 0.060, 95% CI 0.600-0.844). This estimate does not include data for two COYs that were euthanized after their mother died during a

capture operation in 1999. Of 51 yearlings, 28 (55%) survived to be observed with their mothers in the spring census of the year in which they were two-years-old. Mean yearling survival rate was 0.683 (SE = 0.074, 95% CI 0.514–0.821). Yearling survival may be underestimated if females that were observed without their cubs in the spring of their cubs' third year were dissociated from their cubs due to early dispersal of cubs, rather than cub mortality. We do not believe this to be a major detractor from our estimate, however, as we usually observed females during the spring census within days after they and their cubs emerged from dens. We suspect that yearling dispersal prior to denning would not likely favour survival in the central Arctic. Nonetheless, yearling survival increases to 0.902 (SE = 0.047, 95% CI 0.768–0.973) if yearling death is equated only with disappearance sometime during a cub's summer as a yearling (as determined by a fall census), and disappearance prior to the next year's spring census (when cubs have just turned two-years-old) is not equated with death. We could not determine survival of two- and three-year-old cubs as their disappearance between censuses was more likely associated with dispersal, rather than mortality.

4.2.2 Reproduction

Litter size observed in mid-May averaged 2.23 COYs (SE = 0.13, n = 35). We observed six litters of one cub, 16 pairs of twins, 12 sets of triplets, and one litter of four cubs. Yearling litter size decreased to a mean of 1.86 (SE = 0.12, n = 35). Mean litter size of females with two-year-old cubs was 1.85 (SE = 0.15, n = 20).

Mean birth interval was 2.8 years (SE = 0.3, n = 17) and mean reproductive interval was 3.9 years (SE = 0.4, n = 9). The longest reproductive interval was six years. The mean litter size divided by the mean birth interval yielded an annual natality rate of 0.81 COYs per adult female per year. The number of female COYs per adult female per year, to use as n in equation [3.3](section *4.2.3*), was 0.405.

The mean age of first parturition (a) was 8.1 years (SE = 0.5, n = 10). The earliest age of first parturition was 5, indicating that successful mating took place as early as age 4. The mean age of first parturition, where at least one COY in a litter was successfully raised to at least age two, was 8.2 (SE = 0.7, n =5).

4.2.3 Population Rate of Increase

Because data on subadult female survival was sparse, to determine survival to age of first reproduction (l_a) for use in equation [3.3] we used the mean between yearling survival (S_{yrlg} = 0.683) and adult annual survival (S_{adult} = 0.979) for ages 2–4 (i.e., S_{sub} = 0.831), and adult annual survival for ages 5–7. We believed S_{sub} = 0.831 to better approximate true subadult female survival than S_{sub} = 0.600, as obtained from the five bear-years of data that we had for subadult females (section *4.2.1*). Our estimate of l_a (i.e., $S_{COY} \times S_{yrlg} \times S_{sub}^3 \times S_{adult}^3$) was 0.271. From iterations of equation [3.3] with reproductive and survival rates given above, we estimated the population's finite rate of increase, λ, as 1.033.

4.2.4 Density and Population Size

A total of 34 radio-tracked grizzly bears and their cubs were known to visit the 14,000 km^2 regional study area (RSA) in the three years prior to 1997. However, we felt it more appropriate to include only those bears that had significant portions (i.e., more than half the area) of their established home ranges in the RSA in 1997 as "resident" collared bears for the calculation of a density

estimate. Resident bears included six adult females and six adult males plus eight cubs. The estimate for cubs during 1997 included two with G601, two with G652, two with G639, and two COYS supposedly observed with G592 (David Penner, Penner and Associates Ltd., *personal communication*), although this last count may have been for an uncollared bear as G592 was without a functioning radio in spring 1997. We did not count the COY that died with G601 during 1997, the yearling that died with G692, or the yearling that died with G598. The total estimate of collared "resident" bears plus cubs in the RSA in 1997 was thus 20 animals.

To project the total number of uncollared resident bears in the RSA in 1997, we asked David Penner (Penner and Associates Ltd.) to provide us with his estimate of the number of uncollared females that were most likely individual bears in the vicinity of the Diavik/BHP mine sites (i.e., animals that were seen by mine personnel and probably not counted twice). This number was six bears. Because approximately only half of the RSA was covered to get this minimum uncollared female estimate, we doubled the number for the whole RSA to account for the uncovered southern part of the study area (i.e., the uncollared female estimate for the whole RSA was 12 bears). This could be

regarded as a minimum estimate. Based upon the known female:cub ratio obtained from the capture database (36.7% of the captured bears were non-cub females, 32.6% of the captured animals were cubs), we estimated a total of 11 cubs of various ages in the RSA associated with the 12 uncollared females. To project the number of uncollared resident males in the RSA in 1997, we again asked David Penner (Penner and Associates Ltd.) to provide us with his minimum estimate of uncollared males in the Lac De Gras area (n = 3), which we doubled to account for the southern, uncovered portion of the RSA to get an estimate for the entire RSA (i.e., six uncollared males). The total uncollared bear population in the RSA was thus estimated at 29 animals (12 females, six males, and 11 cubs).

For the 14,000 km^2 RSA, the number of collared and uncollared resident bears totalled 49 animals in 1997 (20 collared or associated with collared animals, 29 uncollared). This equates to a minimum density of 3.5 bears per 1000 km^2. Through extrapolation to the entire study area (235,000 km^2), we thus estimated a minimum number of 800 bears to inhabit the region.

4.3 Risk Analysis

4.3.1 Parameters

Parameters incorporated into the RISKMAN program to estimate risks of population reduction were obtained from sections 4.1 and 4.2 above. Because RISKMAN requires an estimate of SE for all parameters, here we used only mean survival rates calculated by the methods of Trent and Rongstad (1974). A common natural adult female survival rate of 0.979 was used for both unencumbered and encumbered females. We used the mean and SE between natural adult and yearling survival as our estimate for natural subadult survival. We calculated the proportion of females with new litters having one, two, or three COYs in their litters to be 0.17, 0.46, and 0.37, respectively. The mean proportion of females that were available for mating in the previous year (i.e., possessed no cubs, or cubs that were at least two-years-old), and then gave birth to a litter, was 0.20 (SE = 0.11, n = 15) for females aged 5–7, and 0.60 (SE = 0.08, n = 42) for females ≥8 years. In our simulations we used a minimum age of reproduction of five years, and a maximum of 25 years. Maximum age for survival was set at 30 years. The mean annual removal of bears from the study area was calculated as 13.4 bears/year. We assume

here that harvest in each year will be composed of the relative proportions depicted in Table 4.2. Associated with the initial population estimate of 800 bears, we ran simulations using SE of 300, 200, and 150 to reflect our uncertainty about this mean. We used the stable age distribution (pre-calculated by RISKMAN) to describe our initial population age structure, because we felt that standing age distributions obtained from capture and harvest records were biased (sections *4.1.1* and *4.1.2*).

4.3.2 Simulation Results

The number of simulation runs leading to set thresholds of population decline appeared quite sensitive to variation in SE of initial population size mean (compare Figs. 4.1 with SE = 300, 4.2 with SE = 200, and 4.3 with SE = 150). However, we believed SE = 200 to best describe the SE associated with our estimate of population size (Fig. 4.2). Translated into a 95% confidence interval, a SE of 200 would result in an interval of approximately 400-1200 about our initial population size of 800 bears.

Using the highest estimates available for natural survival rates and SE of initial population size of 200, we estimated that the probabilities of the current population

declining by 25%, 50%, and 75% over the next 50 years were 0.10, 0.07, and 0.05, respectively (Fig. 4.2). These simulation results were based upon past harvest records detailing the selectivity/vulnerability of different age strata, and a mean of 13.4 bears removed from the population due to harvest per year. These results can be regarded as the "best case" and also most likely scenario, given our current understanding of grizzly bears in the region.

Increasing the harvest rate by six bears annually from 13.4 bears/year dramatically increased the risks of population decline. With a mean of 19.4 bears/year being removed from the population and survival rates entered at the highest rates available, we estimated that the probabilities of the current population declining by 25%, 50%, and 75% over the next 50 years would be 0.42, 0.32, and 0.18, respectively (Fig. 4.4). Here, our initial population size was estimated with a SE = 200.

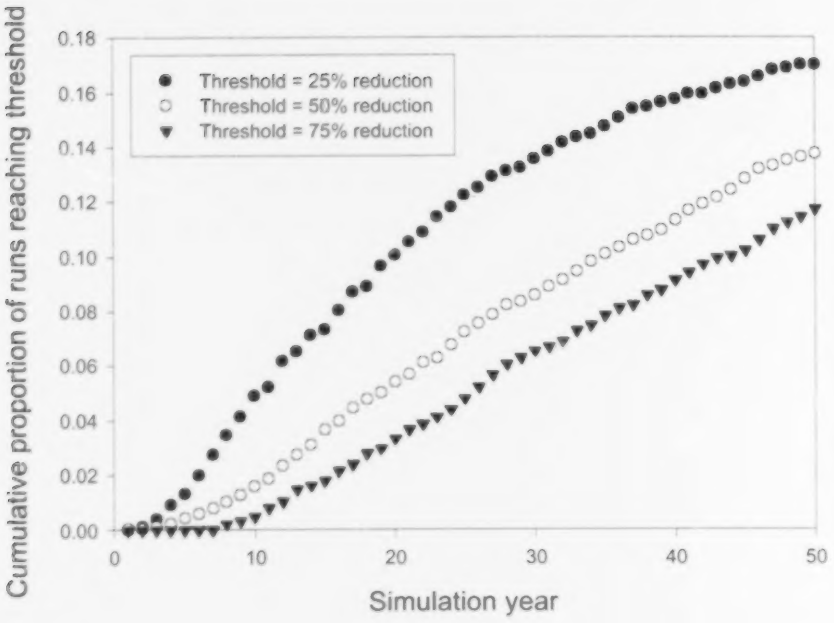

Fig. 4.1 The cumulative proportion of RISKMAN population simulation runs having reached threshold levels of -25%, -50%, and -75% of initial population size as a function of time (future projection). RISKMAN population simulations were performed using the highest survival rates available and an annual removal rate of 13.4 bears/year. Initial population size of 800 bears was estimated with a SE = 300.

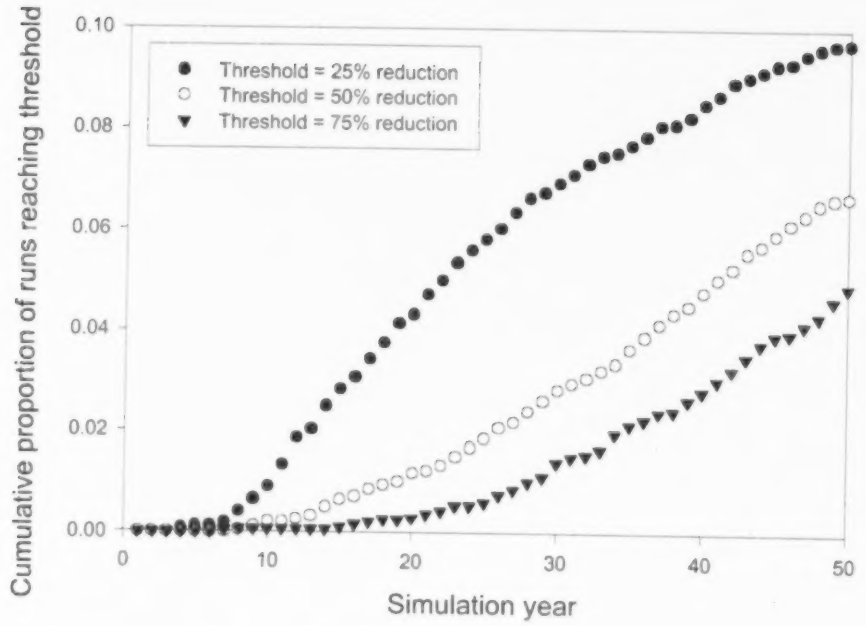

Fig. 4.2 The cumulative proportion of RISKMAN population simulation runs having reached threshold levels of -25%, -50%, and -75% of initial population size as a function of time (future projection). RISKMAN population simulations were performed using the highest survival rates available and an annual removal rate of 13.4 bears/year. Initial population size of 800 bears was estimated with a SE = 200.

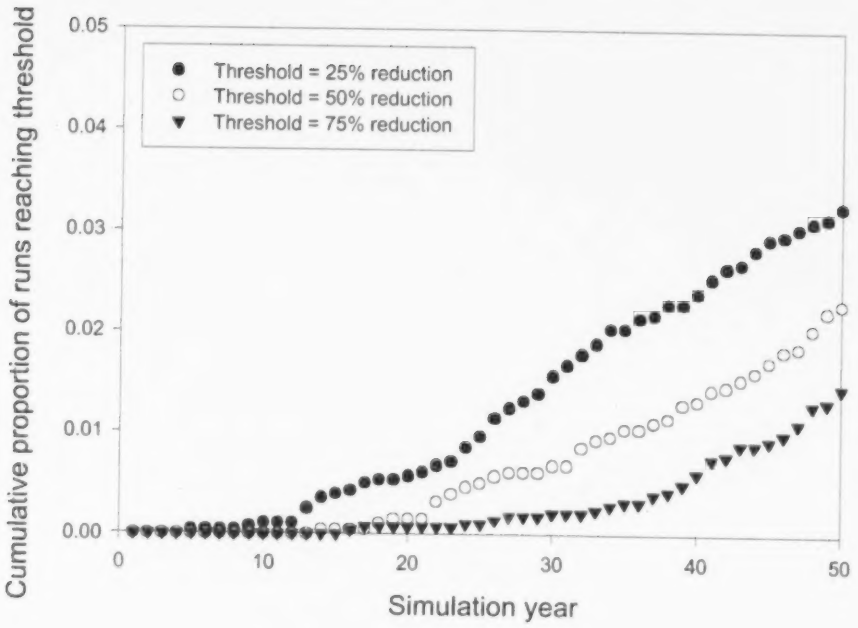

Fig. 4.3 The cumulative proportion of RISKMAN population simulation runs having reached threshold levels of -25%, -50%, and -75% of initial population size as a function of time (future projection). RISKMAN population simulations were performed using the highest survival rates available and an annual removal rate of 13.4 bears/year. Initial population size of 800 bears was estimated with a SE = 150.

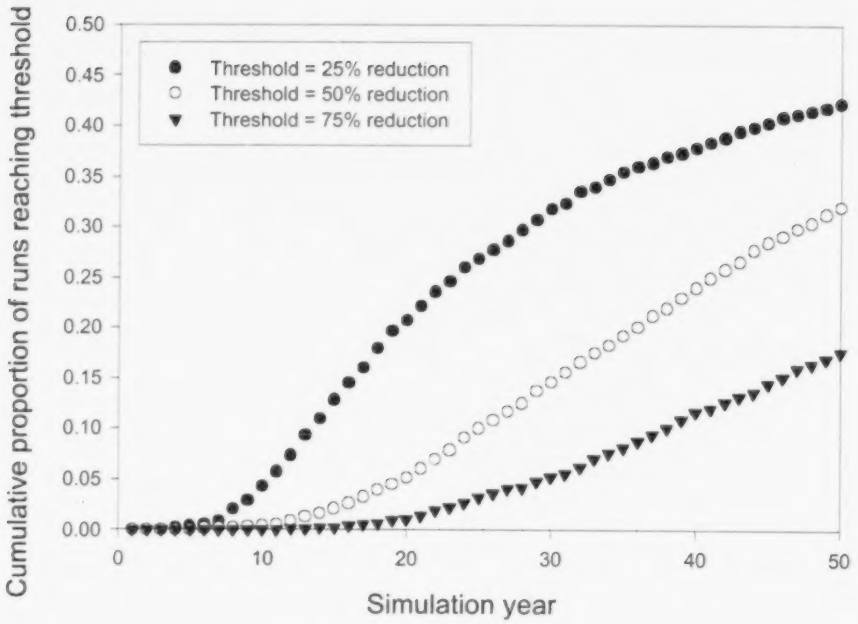

Fig. 4.4 Increasing mean harvest rates from 13.4 bears/year to 19.4 bears/year dramatically increases the risks of population decline. We show the cumulative proportion of RISKMAN population simulation runs having reached threshold levels of -25%, -50%, and -75% of initial population size as a function of time (future projection). RISKMAN population simulations were conducted using the highest survival rates available, as in Fig. 4.2. Initial population size of 800 bears was estimated with a SE = 200.

By including missing bears for which no collar was recovered as unconfirmed natural mortalities in the simulations, and retaining a mean of 13.4 bears/year removed from the population due to harvest, we estimated that the probabilities of the current population declining by 25%, 50%, and 75% over the next 50 years were 0.99, 0.99, and 0.98, respectively (Fig. 4.5). Again, our initial population size was estimated with a SE = 200. These simulation results can be regarded as the "worst case" scenario given the current data we have for grizzly bears in the study area. However, we would caution that this situation is likely underestimating natural survival, but is included here for completeness. Six of seven missing adults disappeared two years after their initial capture and beyond the lifespan of their satellite radio-collars, likely impeding our ability to include them in the spring, 1997 census (Tables 4.3 and 4.4).

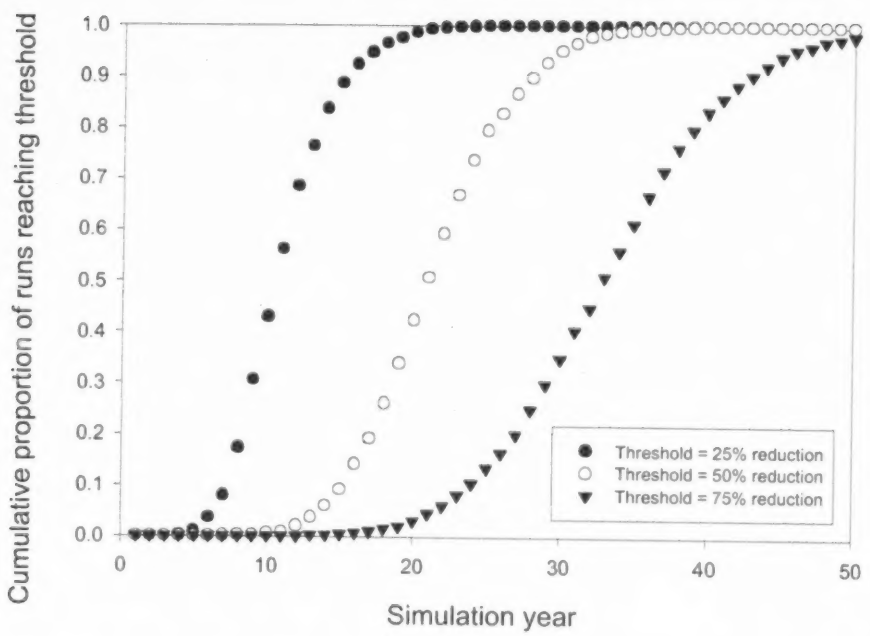

Fig. 4.5 RISKMAN projection simulations with a mean of 13.4 bears/year removed from the population due to harvest (as in Fig. 4.2), but we included missing bears for which no collar was recovered as unconfirmed mortalities in the simulations (n = 7). Presented are the cumulative proportion of RISKMAN population simulation runs having reached threshold levels of -25%, -50%, and -75% of initial population size as a function of time (future projection). Initial population size of 800 bears was estimated with a SE = 200.

5.0 GENERAL DISCUSSION

Ferguson and McLoughlin (2000) concluded that in areas of high altitude (>1000 m) and high latitude (>65° N), populations of grizzly bears respond to extremes in environmental conditions with risk-spreading adaptations. For example, seasonality explained 43% of the variation in age at maturity for Arctic-interior populations of grizzly bears in North America. Populations occurring in these extreme environments are limited by resources; hence, life-history responses should minimize reproductive effort. Female parents decide on the allocation of resources to offspring that reduce the risk of mortality at the offspring level. If parents allocate their resources sequentially in reproductive bouts then they should allocate to a safer, less-productive option in risky environments of extreme variability. The Arctic is characterized by less predictable year-to-year variation and greater interannual (i.e., seasonal) variation (Ferguson and Messier 1996; McLoughlin et al. 2000). Changes in timing of reproduction in life history (e.g., later age at maturity, longer interbirth interval, and greater longevity; Cohen 1970; Philippi and Seger 1989; Sajah and Perrin 1990) and reduced

offspring size and number (McGinley et al. 1987) minimizes the effects of a stochastic environment, such that the geometric fitness is greater (Yoshimura and Jansen 1996).

The grizzly bear population in the central Arctic is near the northern- and eastern-most extent of grizzly bear range in North America. The population is characterized by relatively low density and small bears that live in areas of low productivity and high seasonality (Ferguson and McLoughlin 2000; McLoughlin et al. 2000). We anticipated generally low reproduction resulting from delayed age at first parturition, longer birth and reproductive intervals, and smaller litter size.

As expected, age at first parturition was late compared to other grizzly bear populations (Table 2 in Case and Buckland 1998; Table 1 Ferguson and McLoughlin 2000). However, birth and reproductive intervals were shorter than most northern populations, comparing similarly with intervals of southern interior populations (Case and Buckland 1998; Ferguson and McLoughlin 2000). Further, litter sizes in this study were among the largest recorded for grizzly bears in Canada and Alaska (Case and Buckland 1998). Natality, which reflects both litter size and birth interval, indicated that cub production in the central

Arctic was higher than other barren-ground grizzly bear populations (Case and Buckland 1998). These data suggest that factors other than adaptations to low primary productivity and high seasonality are governing grizzly bear life history in the central Arctic. We looked towards the standing age distributions determined from animal captures and harvest records (Tables 4.1 and 4.2, respectively) to find out one possible reason for the observed life history patterns.

The standing age distribution obtained from captured animals shows a clear bias towards the survival of adult females. In contrast, the standing age distribution obtained from harvest records is almost entirely made of up adult and subadult males, with few unencumbered females and very few females with cubs. This tells us that the total mortality (i.e., natural mortality × human-caused mortality) for males is likely much higher than for females.

As long as there are enough male bears in a population to mate available females, female reproduction will likely be enhanced by reduced numbers of males because of reduced risks from intraspecific predation*. Male grizzly bears are

*But only if the number of subadults in the region does not increase relative to the proportion to the adult males left in the population, a situation that may actually increase the rate of intraspecific predation on females with cubs; Wielgus and Bunnell 1995*a*,*b*). In the

known to prey on females and their cubs (e.g., Jonkel 1987; McLellan 1994). In this study, three radio-tracked female bears were apparently killed by large—likely male—bears. Further, in this study a yearling cub disappeared while the cub and its mother (G592) were followed by an adult male grizzly bear. The mother was observed to mate with the accompanying male shortly after her cub disappeared, suggesting infanticide on the part of the accompanying male. Decreased intraspecific predation may directly affect life history through changes to mortality schedules. Where resources are scarce or unpredictable (i.e., the central Arctic), lower rates of intraspecific predation may indirectly influence life history by allowing females with cubs to exploit higher quality habitats from which they were once excluded by predatory males. Here, life history traits such as adult female size, offspring size, litter size, and reproductive interval may be affected.

McLoughlin (2000) demonstrated that females with accompanying young differed in their habitat selection patterns from adult males in the central Arctic in manner that appeared to minimize their contact with aggressive males. Sexual segregation in habitat selection to lessen

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central Arctic, harvest records indicate that subadult males were

intraspecific predation has also been suggested for grizzly bears in northwest Alaska (Ballard et al. 1993) and Alberta (Wielgus and Bunnell 1995*a*,*b*). In all of these cases, females were displaced by larger males from areas of perceived higher habitat quality to areas of lower habitat quality. Increased availability of quality, male-dominated resources to females with cubs (e.g., in the central Arctic, tall shrub riparian habitats; McLoughlin 2000) would favour offspring survival. Shortened reproductive intervals may then result from increased COY and yearling survival rates, which in the study area were generally higher than for other populations of grizzly bears (mean 60–70%, Bunnell and Tait 1985). Clarkson and Liepins (1993) attributed the long reproductive interval observed near the Anderson-Horton Rivers of the Northwest Territories to the effects of predation on COYs by male grizzly bears. Increased access to higher quality habitats may also permit females to increase investment in somatic growth. Body mass of adult females ($\bar{X}$ = 126 kg, n = 60; from Ferguson and McLoughlin 2000) in the central Arctic averages 10–20 kg more than adjacent barren-ground grizzly bear populations, although it is still relatively low compared to females of southern

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likely not experiencing less harvest mortality than adult males.

interior and Pacific-coastal populations (Table 1 in Ferguson and McLoughlin 2000). Increased body size may account for the larger litter sizes observed in this study, and potentially plays a role in shortening intervals of reproduction by allowing larger offspring at birth or increasing milk production.

The above shifts in life history traits are likely temporary and reversible, brought about by relatively recent (i.e., <50 years) changes in the age structure of males in the population. We are probably observing an integrated plastic response in life history (Stearns 1992). But temporary decreases in intraspecific predation may not be expressed in all of life history traits. To be certain, grizzly bears in the central Arctic exhibit some of the latest ages of first parturition in North America (Case and Buckland 1998; Ferguson and McLoughlin 2000). This suggests that some grizzly bear life history traits are more plastic than others (Stearns 1992). Further, effects of environment on phenotypes (i.e., movement along a reaction norm; Stearns 1992) for litter size and reproductive interval, which can be measured repeatedly during a lifetime, may be more easy to identify than effects on a trait such as age at maturity, which is expressed only once per generation (e.g. sample

sizes for the former traits in a telemetry study will generally be larger than for the latter). Plasticity in grizzly bear life history is remarkable, and is no doubt responsible for the Holarctic distribution of the species.

We believe the population of grizzly bears in the study area to be stable or slightly increasing ($\hat{\lambda}$ = 1.033). However, there is uncertainty about this estimate due to our inability to adequately identify all required parameters from available data. Our estimation of subadult survival (0.831), which is the mean between yearling and adult female survival (excluding capture mortality) for years 2-4, is the greatest potential for bias. We believe this figure to be conservative, however. This figure is at the low end of the range reported by Bunnell and Tait (1985) for other grizzly bear populations, and Hovey and McLellan (1996) estimated subadult survival to be 0.93 in southeastern British Columbia. Hovey and McLellan (1996) concluded that estimation of λ is very sensitive to subadult survival. We are confident that missing radios in this study probably did not translate into animal deaths (six of seven disappeared at the end of radio battery life), and that censoring those radios did not unduly inflate our estimation of finite rate of increase.

We consider our risk analyses with the RISKMAN program to be realistic. Although we believe the population to be currently stable or slightly increasing, we caution that the population is at a definite risk to future population decline, especially if annual removal rates are increased from a mean of 13.4 bears/year. Even if we ignore missing radios in our study as possible deaths, our risk analyses indicate that it is not unlikely that the population of grizzly bears in the central Arctic will decrease substantially within our lifetimes. By adding only six animals to the mean removal rate, there is greater than a 40% chance of a decrease in population size by one-quarter over the next 50 years, up from a 10% chance with current estimates of harvest. These six bears could easily come from increased problem activity at mine sites, or hunt and exploration camps, and may already be present through unreported mortality. In this study, we retrieved from the field three discarded satellite radio-collars, all in excellent condition but opened with all fastening nuts removed. On no other occasions did we find collars with any fastening nuts loose or missing, even those that suffered considerable abuse. We suspect the bears that wore these collars were illegally harvested; however, these harvests

were not included in the harvest records used in our RISKMAN analyses (harvest records from 1958–2000 include a total of only two illegal harvests).

Selectivity/vulnerability rates used in our analyses virtually assume that removed bears from the population will be subadults or adult males, because rates are based on past harvest records. If females with cubs contribute more to the reported harvest than in the past (i.e., as problem kills at mine sites or camps), risks of population decline will likely increase dramatically. We consider the population to be in direct danger of experiencing sustained negative population growth, especially in the context of increasing human activity in the study area.

6.0 RECOMMENDATIONS

Computer simulation models indicate that the population is at risk to population decline, especially if annual removal rates are increased from a mean of 13.4 bears/year. By adding only six animals to the mean removal rate, there is greater than a 40% chance of a decrease in population size by one-quarter over the next 50 years, compared to only a 10% risk of decline under the current reported harvest. Unreported illegal mortality may already be contributing to a higher risk of population decline. We believe that communities, hunting camps, exploration camps, and mine sites must not contribute to a cumulative removal rate exceeding 15 bears/year in the study area. If removal rates exceed 15 bears/year, mitigation may necessitate a reduction in existing harvest quotas. We believe any increase in current harvest quotas would be detrimental to the population. Removal of females (and especially females with cubs) must be minimized from all sources of harvest. This is most important as removal rates used in our risk assessments are based on past patterns of harvest (1958–2000), and thus assume a subadult and male-biased harvest. If females with cubs contribute more to the

reported harvest than in the past (i.e., as problem kills at mine sites or camps), risks of population decline will increase dramatically.

We consider our risk analyses with the RISKMAN program to be realistic. Nonetheless, there is uncertainty in our input parameters, especially regarding subadult survival (of which λ is quite sensitive) and population size (of which model results were sensitive to SE). To refine our models, this uncertainty would need to be decreased; however, both subadult survival and population size are difficult and costly to estimate. Estimating subadult survival would require a tracking study of two- and three-year old bears captured prior to their dispersal from their mother. Subadults in the central Arctic travel over extremely large distances (>20,000 km^2; McLoughlin 2000), and would need to be tracked using expensive satellite radio-collars. Most two- and three-year old bears, however, are probably too small and grow too rapidly to be collared safely.

Estimating population size would be even more costly, and likely involve a lengthy mark-recapture program. Although expensive, a population size estimate using mark-recapture methods would provide not only an objective and more precise estimate of the number of bears in the central

Arctic, but also the means for obtaining new estimates of survival and population rate of increase. Comparing these data with those contained in this report would provide an excellent opportunity to identify the direction of rate of increase for the population. For this reason, perhaps it would be wise to delay estimating population size using mark-recapture methods for some time in the future (e.g., 5-10 years), to permit enough time to lapse between studies to better gauge the effects of current management practices on maintaining the population's rate of increase.

7.0 REFERENCES

Amstrup, S.C., and Durner, G.M. 1995. Survival rates of radio-collared female polar bears and their dependent young. Canadian Journal of Zoology 73: 1312-1322.

Ballard, W.B., Ayres, L.A., Reed, D.J., Fancy, S.G., and Roney, K.E. 1993. Demography of grizzly bears in relation to hunting and mining development in northwestern Alaska. Scientific Monograph NPS/NRARO/NRSM-93/23. U.S. Department of the Interior, National Park Service, Denver, Colorado, USA.

Bunnell, F.L., and Tait, D.E.N. 1981. Population dynamics of bears—implications. Pages 75-98 *in* C.W. Fowler and T.D. Smith, eds. Dynamics of large mammal populations. John Wiley and Sons, New York, New York, USA.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, New York, USA.

Case, R.L., and Buckland, L. 1998. Reproductive characteristics of grizzly bears in the Kugluktuk area, Northwest Territories, Canada. Ursus 10:41-47.

Clarkson, P.L., and Liepins, I.S. 1989. Inuvialuit wildlife studies: grizzly bear research progress report 1987-1988. Technical Report No. 3. Wildlife Management Advisory Council, Inuvik, Northwest Territories, Canada.

Clarkson, P.L., and Liepins, I.S. 1993. Female productivity and cub survival of grizzly bears in the Anderson and Horton Rivers area, NWT, 1987-92. Inuvialuit Wildlife Studies Program Report, Northwest Territories Department of Renewable Resources, Inuvik, Northwest Territories, Canada.

Cohen, D. 1970. The optimal timing of reproduction. American Naturalist 110: 801-807.

Cormack, R.M., Patil, G.P., and Robson, D.S., eds. 1979. Sampling biological populations. Statistical Ecology

Series Vol. 5. International Cooperative Publishing House, Burtonsville, Maryland, USA.

Craighead, J.J., Craighead, F.C., and McCutchen, H.E. 1970. Age determination of grizzly bears from fourth premolar tooth sections. Journal of Wildlife Management 34: 353-363.

Eberhardt, L.L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49: 997-1012.

Eberhardt, L.L., Blanchard, B.M., and Knight, R.R. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. Canadian Journal of Zoology 72: 360-363.

Fancy, S.G., Pank, L.F., Douglas, D.C., Curby, C.H., Garner, G.W., Amstrup, S.C., and Regelin, W.L. 1988. Satellite telemetry: a new tool for wildlife research and management. U.S. Fish and Wildlife Service, Resource Publication 172.

Ferguson, S.H., and Messier, F. 1996. Ecological implications of a latitudinal gradient in inter-annual climatic variability: a test using fractal and chaos theories. Ecography 19: 382-392.

Ferguson, S.H., and McLoughlin, P.D. 2000. Effect of energy availability, seasonality, and geographic range on brown bear life history. Ecography 23: 193-200.

Gau, R.J. 1998. Food habits, body condition, and habitat of the barren-ground grizzly bear. M.Sc. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

Gunn, A., Dragon, J., and Nishi, J. 1997. Bathurst calving ground survey, 1996. Government of the Northwest Territories, Yellowknife, Northwest Territories, Canada.

Harris, R.B., Fancy, S.G., Douglas, D.C., Garner, G.W., Amstrup, S.C., McCabe, T.R., and Pank, L.F. 1990. Tracking wildlife by satellite: current systems and

performance. U.S. Fish and Wildlife Service, Fish and Wildlife Technical Report 30.

Heisley, D. M., and Fuller, T.K. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49: 668-674.

Hovey, F.W., and McLellan, B.N. 1996. Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. Canadian Journal of Zoology 74: 1409-1416.

Jonkel, C. 1987. Brown bear. Pages 457-473 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Kaplan, E.L., and Meier, P. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53: 457-481.

Krebs, C.J. 1999. Ecological methodology (2nd ed.). Addison-Welsey Educational Publishers, Inc., Menlo Park, California, USA.

Lancia, R.A., J.D. Nichols, and K.H Pollock. 1994. Estimating the number of animals in wildlife populations. Pages 215-253 *in* T.A. Bookhout, ed. Research and management techniques for wildlife and habitats. 5th ed. The Wildlife Society, Bethesda, Maryland, USA.

McGinley, M.A., Temme, D.H., and Greber, M.A. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. American Naturalist 130: 370-398.

McLellan, B. 1990. Relationships between human industrial activity and grizzly bears. International Conference on Bear Research and Management 8: 57-64.

McLellan, B. 1994. Density-dependent population regulation of brown bears. Pages 3-34 *in* M. Taylor, ed. Density-

dependent population regulation in black, brown, and polar bears. International Conference on Bear Research and Management Monograph Series No. 3.

McLoughlin, P.D. 2000. The spatial organization and habitat selection patterns of barren-ground grizzly bears in the central Arctic. Dissertation, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

McLoughlin, P.D., Case, R.L., Gau, R.J., Ferguson, S.H., and Messier, F. 1999. Annual and seasonal movement patterns of barren-ground grizzly bears in the central Northwest Territories. Ursus *In press*.

McLoughlin, P.D., Ferguson, S.H., and Messier, F. 2001. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. Evolutionary Ecology *In press*.

Nagy, J.A., Russell, R.H., Pearson, A.M., Kingsley, M.C., and Larsen, C.B. 1983. A study of grizzly bears on the barren grounds of Tuktoyaktuk Peninsula and Richards Island, Northwest Territories, 1974-1978. Canadian Wildlife Service, Edmonton, Alberta, Canada.

Nichols, J.D., Noon, R., Stokes, S.L., and Hines, J.E. 1981. Remarks on the use of mark-recapture methodology in estimating avian population size. Pages 121-136 *in* C.J. Ralph and J.M. Scott, eds. Estimating numbers of terrestrial birds. Studies in Avian Biology 6.

Phillipi, T. and Seger, J. 1989. Hedging one's evolutionary bets, revisited. Trends in Ecology and Evolution 4: 41-44.

Pollock, K.H. 1981. Capture-recapture models: a review of current methods. Pages 121-136 *in* C.J. Ralph and J.M. Scott, eds. Estimating numbers of terrestrial birds. Studies in Avian Biology 6.

Pollock, K.H., Nichols, J.D., Brownie, C., and Hines, J.E. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107.

Pollock, K.H., Winterstein, S.R., Bunck, C.M., and Curtis, P.D. 1989. Survival analysis in telemtry studies: the

staggered entry design. Journal of Wildlife Management 53: 7-15.

Reynolds, H.V. 1980. North slope grizzly bear studies. Alaska Department of Fish and Game, Juneau, Alaska, USA.

Sajah, H., and Perrin, N. 1990. Autumnal vs. spring hatching in the fairy shrip *Siphonophanes grubii* (Dybowski) (Crustacea, Anostraca): diversified bet-hedging strategy? Functional Ecology 4: 769-775.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Macmillan Publishing Company, Inc., New York, New York, USA.

Skalski, J.R., and Robson, D.S. 1992. Techniques for wildlife investigations. Design and analysis of capture data. Academic Press, San Diego, California, USA.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, New York, New York, USA.

Taylor, M., Kuk, M., Obbard, M., Cluff, H.D., and Pond, B. 2001. RISKMAN: risk analysis for harvested populations of age structured, birth-pulse species. *In prep.*

Trent, T.T., and Rongstad, O.J. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. Journal of Wildlife Management 38: 459-472.

White, G.C., and Garrot, R.A. 1990. Analysis of wildlife radio-tracking data. Academic Press, Toronto, Canada.

Wielgus, R.B., and Bunnell, F.L. 1995*a*. Sexual segregation and female grizzly bear avoidance of males. Journal of Wildlife Management 58: 405-413.

Wielgus, R.B., and Bunnell, F.L. 1995*b*. Tests of hypotheses for sexual segregation in grizzly bears. Journal of Wildlife Management 59: 552-560.

Yoshimura, J., and Jansen, V.A.A. 1996. Evolution and population dynamics in stochastic environments. Research in Population Ecology 38: 165-182.